

# Behavioural, Cognitive and Neural Mechanisms of Human Social Interaction

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## **Summary**

Social interaction is a fundamental part of what makes us human and draws on a wide range of neural and cognitive mechanisms. This review summarises current research in terms of four major brain networks. First, the social perception network responds selectively to viewing and interpreting other people's faces and bodies. Second, the theory of mind network is engaged when people think about other people's beliefs and knowledge states. Third, the mirror neuron network has a role in understanding and imitating actions. Fourth, the emotion network shows some selective responding to emotional facial expressions and when people empathise with other's pain. The role of these four networks in dynamic social interactions and real-world communication is also considered.

## **Keywords:**

Human, social, cognitive neuroscience, interaction, social perception, imitation, empathy

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## Section 1: Introduction

Social interaction is a core part of our daily lives, ranging from a baby cooing to her father, to a team playing football or an online video call to negotiate a contract. In all these situations, people are engaging with other people, responding in real time with a complex dynamic that brings together perception, actions, language and motivations. This chapter examines the core mechanisms of social interaction in the brain, and highlights important issues in the field as an introduction to new readers.

Many different domains of research contribute to the study of human social interaction, ranging from conversation analysis

(Stivers et al., 2009) & linguistics

(Levinson, 2016) to basic

neuroscience (Hampton et al., 2008)

and from developmental and clinical

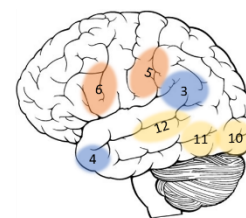
psychology (Happé & Frith, 2014) to

machine learning and artificial

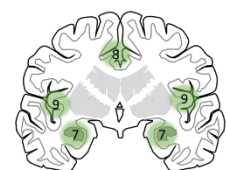
agents (Kopp & Bergmann, 2013).

This overview focuses at the

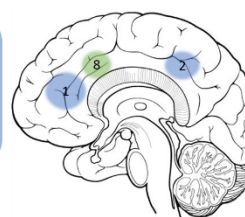
**Mirror neuron network**  
5. Inferior parietal lobe (IPL)  
6. Inferior frontal gyrus (IFG)



**Social perception**  
10. Occipital cortex  
11. Fusiform cortex  
12. Superior temporal cortex



**Mentalizing network**  
1. Medial prefrontal cortex (mPFC)  
2. Precuneus  
3. Temporoparietal junction (TPJ)  
4. Temporal pole



**Emotion network**  
7. Amygdala  
8. Anterior cingulate  
9. Anterior insula

cognitive level, examining the information processing mechanisms involved in different types of social interaction and uses core studies from cognitive neuroscience as a way to organise our understanding of the field. Within the domain of social cognition, many different subtopics have engaged researcher's interest, and many more wait to be probed in detail. In mapping out different subdomains, Happe & Frith (Happé & Frith, 2014) highlight substantial work on person perception, on theory of mind, on empathy and emotion and the sense of self. Similarly, a valuable review from (Kennedy & Adolphs, 2012) identifies key networks in the social brain engaged in emotion processing, theory of mind and person perception. This chapter also organises current research in social neurosciences according to four brain networks which can be linked to four major research themes (Figure 1).

First, the social perception network, including fusiform cortex, lateral occipital regions and superior temporal sulcus (STS), responds robustly when people view image or movies of other people (section 1). Second, the mentalising network, including medial prefrontal cortex (mPFC), temporal poles, precuneus and temporoparietal junction (TPJ), responds when participants think about other people's thoughts and beliefs (section 2). Third, the mirror neuron network including inferior parietal cortex and inferior frontal gyrus, responds when people perform actions, observe actions and imitate actions (section 3). Fourth, the emotion network including amygdala, anterior cingulate and anterior insula responds in different emotional states (section 4). Reviewing these four networks allows us to examine core mechanisms of social interaction in the brain. Note that research on intergroup relationships (Merritt et al., 2021) including conflict, affiliation and morality (Crockett, 2013) as well as work on vocal (Scott, 2019) and tactile (Cascio et al., 2019) social interactions, will not be covered in the current chapter.

## Section 2: Social perception

Socially relevant stimuli can be experienced in all sensory modalities but this review will focus on visual stimuli. A core question in this area is the question of domain specificity – are there brain regions which are dedicated and specialised for the perception of social stimuli, or is processing of social and non-social information mixed within the same general system? Pioneering work from Kanwisher and colleagues established the idea that there might be specific brain systems dedicated to social perception that do not respond to non-social stimuli. They identified a brain region in the ventral visual pathway which is robustly engaged when participants see images of faces, but not to houses or objects (Kanwisher et al., 1997), and labelled this the *fusiform face area*. More recent research has identified a broader face network including occipital face area (Haxby et

al., 1999). Research on face perception over the last 20 years has examined the question of how we recognise and process faces, as well as the specific role of FFA in these processes. Studies have shown precise encoding of facial identity in the FFA using both repetition suppression (Winston et al., 2004) and multivoxel pattern analysis methods (Axelrod & Yovel, 2015). These ideas are consistent with the claim that the human brain encodes faces in a structured 'face space' (Valentine, 1991; Valentine et al., 2016) in which similar faces are coded in a similar way. Behavioural evidence shows that people can recognise a caricature which exaggerates an individual's distinctive features better than the true face (Lee et al., 2000). These results are all in-line with a broader claim that 'faces-are-special', and that the FFA contains a specific neural mechanism which is dedicated to and evolved for the recognition of human faces (Kanwisher, 2000) and which does not process any other stimuli.

However, a rival model for face processing is also possible. The configural expertise model (Gauthier et al., 1999b) claims that, due to social experience, everyone has expertise in recognising faces and the engagement of FFA reflects the fine-grained processing needed to distinguish similar items within any expert category. According to this model, within-category visual recognition by an expert, for example of birds or cars (Gauthier et al., 2000) should engage the same brain systems as face recognition. Initial evidence for this came from studies of the recognition of artificial creatures called greebles – after learning greeble recognition over a period of weeks, participants show greeble inversion effects and engage FFA when viewing greebles (Gauthier et al., 1999a). More recent meta-analyses (Burns et al., 2019) support the importance of expertise in the FFA, and these ideas are in line with broader models of face processing (Haxby et al., 2000) which demonstrates how face perception extends beyond the FFA and links to other brain systems for social perception of gaze, facial movements and visual speech.

An alternative way to study face perception is to examine development and individual differences. Face selectivity seems to be present from birth in humans, as neonates prefer to view a face-like stimulus where two eyes with black pupils are positioned over a mouth, in comparison to other matched stimuli (Farroni et al., 2005). However, the development of face recognition is slower – 6 month old infants can learn to recognise by human and monkey faces, but by 9 months of age, infants are better at recognising humans (Pascalis et al., 2002). This indicates that, over the first year of life, infants develop perceptual tuning to the human faces around them. Early face exposure is important for later development, as adults who had cataracts in infancy that limited their visual acuity from birth to around 2 months of age (when the cataracts were removed) still have subtle differences in their face perception abilities in adulthood (Le Grand et al., 2001). This suggests there may be a critical period where the development of face perception requires visual inputs of faces. A

study which raised infant monkeys with interactive care but no visual access to faces also found reduced face discrimination abilities in the monkeys (Sugita, 2008). Altogether, these developmental studies suggest that infants are highly attuned to faces and attend to them from birth, using the first year of life to develop strong face recognition skills.

However, in some people, face recognition is impaired or fails to develop. Acquired prosopagnosia occurs when brain damage in adulthood causes a specific difficulty with the recognition of faces (Riddoch et al., 2008). Developmental (or congenital) prosopagnosia occurs when an individual has exceptionally poor face recognition skills from birth, without any known brain damage (Behrmann & Avidan, 2005; Susilo & Duchaine, 2013). People with DP are often good at recognising objects, even for subtle discriminations within a category, but perform very badly on face recognition tests and report relying on non-face features (voice / gait / hairstyle etc) to recognise people in real life. However, some researchers argue that DP is a general visual deficit and is not specific to faces, for example, people with DP may perform poorly on global information processing tasks (Avidan et al., 2011). Family tracing studies of DP (Grueter et al., 2007) and twin studies (Wilmer et al., 2010) suggest relatively high heritability of face recognition abilities, which is consistent with the idea that there are specific evolved brain systems for face recognition. One might expect neuroimaging studies to localise these to the FFA. However, FFA responses can often be seen in people with DP (Avidan et al., 2005). Other studies suggest there are differences in more subtle FFA signals, as these signals allow face discrimination by MVPA in typical but not in DP participants (Zhang et al., 2015). Connectivity differences from FFA to frontal cortex have also been identified in DP (Thomas et al., 2008). To summarise, studies of disorders of face perception suggest that there are robust individual differences in this ability, but debate continues over whether this indicates a special brain mechanism dedicated to face processing or a more general perceptual expertise system.

The perception and identification of static faces is not the only aspect of visual processing that matters for real world social interaction. It is also important for people to recognise and respond to gaze behaviour, facial expressions, body posture, hand movements and more. Different cognitive processes and brain networks have been identified in relation to each of these different types of social perception. These include regions specialised for hand perception (Bracci et al., 2010), body perception (Peelen & Downing, 2007), gaze (Carlin et al., 2011) and mouth movements (Pelphrey et al., 2005), though there may be overlap between many of these (Allison et al., 2000). It has recently been suggested that the superior temporal sulcus provides a third visual pathway (in addition to established pathways for object recognition and for action), which is specialised for social

perception (Pitcher & Ungerleider, 2021). The degree to which these regions provide for conceptual-level representations of people and actions (Tucciarelli et al., 2019) is also still debated.

While traditional approaches to the study of social perception show participants carefully controlled stimuli that manipulate a single aspect of perception, an alternative method is to explore brain responses to natural stimuli such as Hollywood movies or popular TV shows. These rich audiovisual stimuli are created to engage people in a compelling story (Hasson & Landesman, 2008) and can engage a wide range of brain systems within and beyond social perception networks. Analysis of brain responses to movies typically relies on inter-subject correlations, (Hasson et al., 2004), in which the time course of activity in each voxel for one participant's brain is correlated with the same voxel in another person's brain. Peaks in these correlations reflect times when a brain region is consistently engaged by the movie stimuli, for example, peaks in FFA tend to occur when faces are present on the screen. In addition, stronger correlations are seen between brains when participants have the same recall of a complex story (Chen et al., 2016), indicating that inter-subject correlations reflect the interpretation of a stimulus as much as the sensory inputs. Overall, these methods using richer more naturalistic stimuli are providing new insights into the integration of brain systems for social perception, and can be used in conjunction with more traditional methods to make sense of the neural mechanisms of human social perception.

### Section 3: Theory of Mind

Theory of mind, also known as mentalising, is a core component of human social cognition. The term 'theory of mind' was coined in a paper by (Premack & Woodruff, 1978) which asked if a chimpanzee can understand what another person thinks. The core test of 'theory of mind' is the ability to understand false beliefs, for example, to recognise that if Sally last saw her ball in a basket and did not see Anne move it to the box, then Sally will falsely believe the ball is in the basket (Wimmer & Perner, 1983). Typically, children show a dramatic change in performance of this classic Sally-Anne task over the preschool years, as 3 year olds consistently give the incorrect answer and 5 year olds are consistently correct. This is part of a developmental progression in children's performance on theory of mind tasks (Wellman & Liu, 2004) as they gradually acquire stronger skills in reasoning about other people's beliefs. However, there is also evidence that much younger children have some ability to engage in belief processing. A landmark study from (Onishi & Baillargeon, 2005) used a non-verbal theory of mind task in which 15 month old infants watched an adult who had a false belief about the location of a toy reach for the object. They found evidence that the infants were surprised (and look longer) when the adult reached for the true location of the

toy (inconsistent with her false belief) and a number of studies have found similar effects in infants (Kovacs et al., 2010; Southgate et al., 2007).

These claims that theory of mind skills might be available to very young, preverbal infants stands in stark contrast to the failures of 3 year olds on the classic Sally-Anne task and are still controversial. Some researchers argue that infants do not really have a theory of mind, but use general attentional mechanisms to succeed on these tasks (Heyes, 2014) but one plausible explanation suggests that there are two different types of theory of mind. (Apperly & Butterfill, 2009) proposed that infants have access to a simple *implicit* theory of mind which can rapidly perform simple belief calculations, for example about whether an object is present or absent, but which would fail in more complex contexts. They also suggest that children over 4 years old also have an *explicit* theory of mind which can perform slower more complex belief calculations (e.g. he knows that she thinks the apple is in the basket). Such explicit performance seems to depend on language skills (Astington & Jenkins, 1999) and exposure to thinking about other people's minds (Hughes et al., 2018). However, even adults might still make use of their rapid implicit system in simple tasks such as visual perspective taking (Furlanetto et al., 2016).

Studies of the neural mechanisms of mentalising have been remarkably consistent over the last 30 years. An initial PET study in which participants read stories that did / did not involve mental states identified the medial prefrontal cortex, temporoparietal junction and temporal poles as core brain regions for theory of mind (Fletcher et al., 1995). These findings have been replicated in many studies since, with precuneus now added to the ToM network; see (Schurz et al., 2014) for a detailed meta-analysis. Studies which pinpoint the processing of false belief information often link this very specifically to the temporoparietal junction (Saxe & Kanwisher, 2003) and brain damage to this region impairs performance on non-verbal theory of mind tasks (Samson et al., 2004). Recent studies of implicit false belief tasks show engagement of the same brain regions (Boccardoro et al., 2019; Schneider et al., 2014). Single neuron recordings from prefrontal cortex of adults undergoing brain surgery has even identified individual neurones which encode another person's beliefs (Jamali et al., 2021). Thus, there is strong evidence that this ToM network is engaged in the calculation of another person's belief, including cases where this differs from one's own belief.

Engagement of ToM regions of the brain can also be seen in more interactive tasks, when belief computations are being used. An early study showed that participants engage medial prefrontal cortex when playing a game of rock-paper-scissors against a human but not when playing against a computer (Gallagher et al., 2002). An important paper from (Hampton et al., 2008) had participants in fMRI play a competitive game with another person outside the scanner. On each

trial, the participant would win if he made a *different* choice to the other player, but the other player would win if he made the *same* choice, and thus the payoff matrixes for the two people are opposed. People playing this type of game typically show a complex dynamic pattern of choices, and Hampton developed an elegant mathematical model which could capture this, modelling how each player calculates their influence on the other player's behaviour. The model parameters could then be fit to the brain imaging data, showing a close link between regions of the ToM network and the computational parameters which explain behaviour. A recent replication (Konovalov et al., 2021) gave participant the same task framed either as a social interaction with another person or as an asocial interaction with a machine. Engagement of TPJ depended on both the social context and the behaviour of the partner, while mPFC reflected mainly the strategy of the player. This type of study takes us closer to understanding the specific computational mechanisms which are being implemented within the ToM network.

The study of the neuroscience of ToM is also closely linked to our theories of autism. Autism is a neurodevelopmental disorder which affects around 1 in 100 people in the UK (Baron-Cohen et al., 2009). Diagnosis is based on difficulties in social communication / social interaction such as atypical eye contact, language use and nonverbal interactions, and also the presence of repetitive behaviours and restricted interests which can include motor or verbal stereotypies, rigid routines and narrow focused topics of interest (American Psychiatric Association, n.d.). As recognition of autism has increased over the last decades, awareness of the massive heterogeneity of this diagnosis and the range of comorbidities present has also increased. Some people with autism also have learning difficulties (but others have high IQ), and many also have social anxiety, ADHD, oppositional-defiant disorder, mood disorders and other diagnosis (Simonoff et al., 2008). Most adult research studies focus on the sub-population of autistic participants with normal IQ, while many child and infant studies include a wider range of participants. Thus, it is challenging to make any generalisations about people with autism.

Despite these challenges, if autism is to be understood on a neurocognitive level, it is important to focus on core difficulties that might distinguish autism from other neurodevelopmental disorders. A large number of different theories have been proposed to account for the core social and non-social features of autism in different ways. This chapter focuses only on the ToM approach to autism, a review of other approaches is here (Rajendran & Mitchell, 2007). The original ToM theory of autism built on the finding that autistic children often fail the false-belief tasks (Baron-Cohen et al., 1985), and suggested that difficulties in false belief calculations could account for atypicalities in social interaction and communication in autism (Frith et al., 1991). For example, difficulties in mentalising could account for why autistic children find it hard to deceive others



(Sodian et al., 1992) and to pick the most relevant information in communication tasks (Deliens et al., 2018; Frith, 2003). This theory has been supported by more recent data showing reduced use of implicit theory of mind in autistic adults (Senju et al., 2009) and reduced brain activation in ‘mentalising’ regions of the brain during theory of mind tasks (Frith, 2001; White et al., 2013). An important study of a large sample of adolescents with & without autism suggests that ToM skills correlate with both social and non-social behaviour (C. R. G. Jones et al., 2017), but the cognitive mechanisms by which ToM difficulties could cause changes in non-social cognitive skills remains unclear. The heterogeneity of autism remains a major challenge for cognitive research and it is possible that there is no one mechanism underlying autism (Happé et al., 2006).

## Section 4: Mirror neurons

Landmark papers in the 1990s (di Pellegrino et al., 1992; Gallese et al., 1996) reported the existing of mirror neurons in the premotor cortex of the macaque monkey. These neurons respond selectively when the monkey performs a particular hand action (e.g. grasping a peanut) and also when the monkey sees a person perform the same hand action, thus encoding the similarity between self-actions and observed actions, like a mirror. Later reports documented mirror neurons in the inferior parietal lobe as well, and showed selectivity for goal directed actions (Fogassi et al., 2005). Human neuroimaging studies report activations in premotor cortex / inferior frontal gyrus and inferior parietal cortex when participants view actions, perform actions and imitate actions (Caspers et al., 2010). Though traditional fMRI methods cannot show that individual neurons in the human brain have mirror properties, studies using both repetition suppression (Kilner et al., 2009) and multi-voxel pattern analysis (Oosterhof et al., 2010) provide fine-grained evidence that is consistent with the existence of mirror neurons in the human brain. Thus, these regions are commonly referred to as the human mirror neuron system.

Since the discovery of mirror neurons, there has been a substantial debate about the origins of mirror neurons, their function and their contribution to broader social cognition. Initial claims that mirror neurons might provide a basis for a wide range of social abilities such as theory of mind (Gallese & Goldman, 1998), empathy (Iacoboni, 2009) and language (Pulvermüller & Fadiga, 2010) seem unlikely to be true (Heyes & Catmur, 2022) and more recent work has focused on the role of mirror neurons in understanding and imitated actions, as well as the origins of these systems. This chapter reviews first the debate about ontogeny and then function.

The debate about the origins of mirror neurons has focused largely on the origins of imitation – if imitation behaviour is innate, this would imply that mirror neurons are also innate and

thus were specified by evolution for a social purpose. To imitate another person's action is a challenging behaviour – the infant must be able to interpret the visual image of the adult on the retina and produce a complex pattern of activation in the motor system that will result in a similar movement of the infant's own face or hand. Early evidence suggested that newborn humans (Meltzoff & Moore, 1977) and macaques (Ferrari et al., 2006) might imitate the facial actions of an adult, for example tongue protrusion or mouth opening actions. However, there are several limitations to this work. Infants produce tongue-protrusion responses to many different stimuli (e.g. bright lights), not just when seeing an adult perform tongue-protrusion (S. S. Jones, 1996) and they do not reliably imitate other actions (Anisfeld, 1996), so the specific matching of visual to motor does not seem to be present in neonates. A recent large-scale study of over 100 infants (Oostenbroek et al., 2016) found no evidence of robust and specific imitation in the first weeks of life, and thus it seems unlikely that infants are born with the ability to imitate.

In contrast, there is evidence that infant's ability to imitate adults develops over the first year of life and is not reliably present before 8 or 10 months (S. S. Jones, 2007) while tongue-protrusion is not copied until 18 months. This implies that neural systems supporting imitation, including mirror neurons, develop gradually over this time period. (Cook et al., 2014) provide a detailed model of how mirror neuron systems could arise from general sensorimotor learning over the first year. Studies of infant behaviour shows that they spend a substantial amount of time gazing at their own hand and being imitated by a parent or carer (Ray & Heyes, 2011), both of which provide valuable inputs for the infant to learn to associate the visual image of an action with the motor sequence that causes that action. For example, by gazing at her own hand and performing random movements, the infant can learn the association between the visual image of a particular hand-shape and the motor command needed to make that hand-shape, as specified in mirror neurons. For hand-shapes, learning from self-observation can then generalise to other people's hands, while for face-actions the experience of being-imitated by an adult may be particularly important. Both infants (de Klerk et al., 2014) and adults (Cross et al., 2006, 2009) show stronger brain activation patterns to learnt action sequences, in line with the claim that learning is critical to the ontogeny of mirror systems (Cook et al., 2014).

Moving beyond infancy data, it is interesting to consider what mirror neurons might do for human social cognition and social interaction, that is, what function do they serve? Two major roles seem plausible in typical adults – understanding the actions of others and imitating those actions. First, the *understanding model* claims that mirror neurons allow people to understand another person's action 'from the inside' (Rizzolatti et al., 2001). These models draw on the simulation theory of mentalising, which suggests that the best way to understand another person is to imagine

what they are doing and thinking. Mirror neurons could provide a mechanism which matches the actions of another person to one's own motor representations and thus allow the observer to understand the goals and intentions of another person by simulation (Gallese & Goldman, 1998). However, this approach has been criticised as many actions cannot be interpreted from only motor information (Jacob & Jeannerod, 2005). Studies of the role of mirror systems in understanding actions show that it is important to distinguish between different types of understanding – discriminating a hand-shape is not the same as interpreting what object a person is grasping or why they are grasping (Grafton & Hamilton, 2007). Different regions within and beyond the mirror system seem to contribute to these different types of action understanding. Mirror neuron regions are important in tracking the precise kinematics of actions (Pobric & Hamilton, 2006) and to track simple action goals (Hamilton & Grafton, 2006) but not other aspects of action understanding. Perceptual processing of actions in lateral-occipital regions and STS is also important (Lingnau & Downing, 2015), and explicitly asking people to judge action intentions engages TPJ and mPFC in the mentalising network, not mirror systems (Spunt et al., 2010). Thus, mirror neuron systems may contribute to understanding actions but are likely to work with other brain systems to do so.

Mirror neuron systems are also believed to have a critical role in imitation, including imitation learning and imitation for social bonding. Many studies show activation of MNS regions when participants imitate simple finger movements (Iacoboni et al., 1999) and when they learn by imitation (Buccino et al., 2004). However, this is not the whole story. The MNS is equally engaged in contexts in which participants imitate and when they perform complementary actions (Newman-Norlund et al., 2007). This implies that MNS regions may be engaged in general sensorimotor mapping, and that the activation of these regions for imitation may be similar to that for other familiar visuomotor tasks including complementary actions and actions on objects (Hamilton, 2016). Few studies have directly tested the importance of the MNS in imitation in comparison to matched non-imitative visuomotor tasks, but one careful examination of delayed imitation found activation of extrastriate cortex rather than traditional MNS regions (Makuuchi, 2005). Neuropsychological studies of the impact of brain damage on imitation behaviour show that damage to frontoparietal cortex, including but not only mirror neuron regions, causes difficulties in gesture imitation (Lesourd et al., 2018). Overall, these studies suggest that the MNS may contribute to imitation behaviour and imitation learning but is not the only brain system that is important.

Thinking about human imitation behaviour more generally, it is clear that humans have a strong capacity for imitation and will often copy actions that are unnecessary (Lyons et al., 2007) which is termed 'overimitation'. Apes do not engage in this behaviour (Clay & Tennie, 2018) and children overimitate more in social contexts (Marsh et al., 2014). Human imitation behaviour is also

highly social – adults spontaneously imitate meaningless actions in contexts of affiliation (Chartrand & Bargh, 1999) and children’s imitation is similarly modulated by social factors (Over & Carpenter, 2013). Thus, it seems that imitation is not solely about learning new information, but people also imitate in order to connect with others and form social bonds (Chartrand & Lakin, 2013). Recent studies showing that people imitate more when they are being watched (Krishnan-Barman & Hamilton, 2019; Marsh et al., 2019) implies that imitation behaviour can be used as a social signal to enhance affiliation (Wang & Hamilton, 2012).

However, such signalling must be tightly controlled, and people are also good at inhibiting imitation behaviour and choosing when not to imitate. Damage to prefrontal cortex can cause excessive imitation (Brass et al., 2003). Neuroimaging studies of the control of imitation demonstrates a key role for mPFC (part of the mentalising network) in this behaviour (Brass et al., 2005). When a context of eye-contact enhances mimicry, then mPFC provides top-down modulation of the MNS (Wang et al., 2011). Overall, these data show that the MNS has a role in both understanding actions and in imitating actions, but that it does not work alone. It is closely linked to other social information processing network and its major functions are implemented in conjunction with these systems.

## Section 5: Emotion & empathy

The study of human emotion, social communication of emotion and empathy is a rapidly evolving area of research. For decades, our model of emotion processing has been dominated by Ekman’s claims that six basic emotions (happy/sad/fear/anger/disgust/surprise) are associated with six distinct physiological states of the body and six distinct facial expressions that provide a ‘read-out’ of a person’s internal emotional state and which are universal across cultures (Ekman, 1992). It is becoming increasingly clear that this position does not hold (Feldman Barrett et al., 2019), and that facial expressions may be a more complex mixture of communications (Crivelli & Fridlund, 2018) and responses to the world (Susskind et al., 2008). The behavioural ecology view of facial communication (Crivelli & Fridlund, 2019) provides one possible alternative to understanding facial emotions. This section first examines whether studies of brain systems engaged in experiencing and perceiving emotions align with Ekman’s model, and then considers neural mechanisms of pain and empathy.

For some emotional states, there is a relatively straightforward mapping between the context which induces the emotion, the internal feeling, the neural activation patterns, the associated facial expression and the social response to seeing that expression in another person.

The best example is disgust. Noxious and disease-related stimuli induce a visceral disgust reaction together with a nose-wrinkled/eyes closed facial expression that may be an attempt to reduced exposure to the disgusting item (Rozin et al., 2008). When participants experience disgust in an fMRI scanner (induced by smells), there is robust engagement of anterior insula and the same region is also activated when participants see a disgust expression on another person's face (Gan et al., 2022; Wicker et al., 2003). Thus, this particular emotion seems to fit the pattern predicted by Ekman.

A second emotional state which might seem to fit Ekman's pattern is fear. A fear face has a clear configuration with wide eyes and the white of the sclera visible and it is hypothesised that this facial configuration maximises the information a person can receive from the environment to identify threats (Susskind et al., 2008). Viewing fear faces robustly engages the amygdala (Costafreda et al., 2008; Morris et al., 1996) and being placed under threat also engages this brain region (Phelps et al., 2001). A unique participant with bilateral damage to the amygdala – patient SM – has difficulty recognising fear faces and reports a lack of fear when presented with fear-related stimuli such as snakes and spiders (Feinstein et al., 2011). Finally, people are able to learn by seeing events where another person expresses fear, and the amygdala is again involved (Glenn et al., 2012; Olsson & Phelps, 2007). Thus, there might seem to be a clear link between self-experienced fear, perceived fear and engagement of the amygdala. However, a closer look at the data shows things are not so simple. The activation of the amygdala might be driven by 'wide-eyes faces' including surprise faces (Vrticka et al., 2012) and patient SM seems to recognise fear stimuli that do not involve wide-eyes (Feldman Barrett, 2018). Furthermore, the amygdala is made up of many sub-nuclei which may have different functions (LeDoux, 2007) and in associative learning tasks in relation to an 'associability' parameter that tracks how well participants can learn about items (Li et al., 2011). Thus, there is no simple one-to-one link between the amygdala and fear, and it is certainly not possible to infer a person's experience of fear by measuring engagement of their amygdala (Poldrack, 2011).

This summary suggests that disgust and fear might conform to Ekman's idea of basic emotions; each of these states has a specific trigger in the environment, a distinct physiological state and a facial configuration which minimises or maximises exposure to the environment. Furthermore, there is evidence of self-other overlap for both the perception and production of these two emotions, with the same brain regions engaged for experiencing and perceiving disgust (anterior insula) and for experiencing and perceiving fear (amygdala).

However, for other emotions, things are not so simple. It is often assumed that the emotion 'happy' is conveyed by a smile, but there are many different types of smile: Duchenne smiles engage

muscles near the eyes while non-Duchenne smiles do not, and the former are considered as more genuine (Gunnery & Ruben, 2015). Furthermore, people often produce different types of smiles in contexts of embarrassment (Keltner, 1995) or pain (Prkachin & Solomon, 2008), and three different types of smiles can be used to communicate reward, affiliation or dominance in social relationships (Martin et al., 2017). Thus, there is no straightforward mapping between a smile and an internal emotion. Rather, smiles are a good candidate for a social-communication signal (Crivelli & Fridlund, 2018). They are produced more when others are watching (Fridlund, 1991) and vary according to many subtle social dimensions. Thus, Ekman's claim that emotions provide a facial read-out of a specific internal state does not seem to hold for all emotions.

Studies of the perception of emotion also illustrate the complexities of this area. Using complex computer-generated stimuli which were rated by observers from different countries, Jack et al found that Asian participants judged emotions differently (Jack et al., 2012), and that faces were best classified into four emotions rather than six (Jack et al., 2016). Studies of the use of emotional faces in real-world contexts suggest that it is possible to distinguish as many as 16 different emotions from YouTube videos (Cowen et al., 2020). In contrast, when only intense peaks of emotional events are examined, observers find it hard to discriminate even the valence of the emotion (Aviezer et al., 2012). For example, the intense expression on the face of a tennis player who has just won a major tournament cannot be distinguished from the expression of a player who has just lost. These studies all highlight the complexity of facial movement in real world communicative contexts and suggest that our research must move beyond the idea of just six emotions and towards richer communicative models (Crivelli & Fridlund, 2018).

One emotion which does not feature prominently in Ekman's model, but which is very important in evolutionary terms, is pain. Pain is compelling signal with specific peripheral nerves which bring pain signals rapidly to the brain to avoid harm. A robust network of brain regions is engaged when a person experiences pain including primary somatosensory cortex, anterior cingulate and anterior insula (Garcia-Larrea & Peyron, 2013). These are commonly referred to as the 'pain matrix' and activation of AI and ACC correlates with the subjective experience of pain (not the physical intensity) (Rainville, 1997). Although there is no single facial expression associated with pain, the ability to perceive that another person is in pain is a critical step towards feeling *empathy* for that person. There is a large body of work on the neural and cognitive mechanisms of empathy and what they might mean for our social functioning.

The term *empathy* is used in different ways in different papers, but the definitions from Singer et al (Bernhardt & Singer, 2012) provide a useful distinction between emotional contagion

(feeling the same emotion without regard to the source), empathy (feeling the same emotion but knowing another person is the source) and compassion (feeling motivated to assist someone in pain). Feeling empathy is also distinct from emotion recognition, that is, it is possible to put a verbal label on an emotional state without sharing it, or to share an emotional state without being able to label it (Bird & Viding, 2014). The term empathy has been applied to all of these different processes, but following Singer we restrict it to only the case of sharing an emotion experienced by another person, with a focus on the experience of pain.

Neuroimaging studies of empathy typically measure brain activity in contexts where participants know that another person is in pain. For example, when participants see images or videos depicting a painful context such as fingers caught in a door, there is activation of AI and ACC which correlates with rating of pain intensity (Jackson et al., 2005). Similarly, when participants in fMRI saw a green arrow that signalled 'you will receive a painful shock' or a red arrow that signalled 'your long-term partner who is sitting beside you will receive a painful shock', then AI and ACC were engaged in both conditions (Singer et al., 2004). Recent meta-analyses confirm that AI and ACC together with somatosensory and inferior frontal regions are robustly activated in empathy and pain perception (Fallon et al., 2020). These results suggest that there is overlap between self and other for the emotional experience of pain and sharing of pain with another person. This is in line with a general simulation theory of social cognition, as self-other overlap has been found for pain as well as disgust, fear and actions. The general principle that neural mechanisms which are engaged for a self-experience are also active when observing someone else experience the same thing seems to apply across a range of contexts. However, it is important to be cautious and avoid claims that measuring brain activation can quantify an individuals' empathy or understanding of another person. There is much more we need to know about how pain states are shared and communicated in order to develop a real-world neuroscience of empathy.

## Section 6: Interaction & communication

The sections above outlined four major brain networks which are important for human social cognition and social interaction, and where robust results have been found. These networks for social perception, mentalising, emotion and action allow people to respond appropriately to a wide range of social events. In the last decade, more research has begun to examine the integration of these networks in more complex contexts. In particular, situations where people do not just passively observe stimuli in an MRI scanner, but must actively respond to another person, are an important research focus. This includes studies that take neuroscience 'into the wild' and 'out of

the lab' using alternative neuroimaging methods such as functional near-infrared spectroscopy (fNIRS) and electroencephalography (EEG), as well as studies that create interactions within the MRI scanner. This final section highlights recent advances in this domain and potential future directions for research that integrates across brain networks.

An important example of why research needs to move beyond the traditional method where a solo participant views well-controlled stimuli in the lab can be seen in the study of gaze. In traditional gaze cuing studies, participants see a face gazing left or right and must respond with a keyhit to a star appearing to the left or right – reaction times are reliably faster when the face gazes towards the target location (Frischen et al., 2007). However, this effect is substantially stronger if the participant believes they are viewing the face of a real person (over a live video connection) (Teufel et al., 2010). When viewing an image of a human face on a computer screen, participants typically look at the eyes (Birmingham et al., 2008), but they are aware that the person in the video cannot see them (Risko et al., 2016). When social attention is measured in real-world contexts, behaviour is very different to the lab. For example, participants gaze less towards the eyes during encounters with a real person versus a video (Cañigüeral et al., 2020; Laidlaw et al., 2011). People also show audience effects when they believe they are being watched (Izuma et al., 2010) which differ with context and personality (Uziel, 2007). Changes in behaviour when being watched are believed to arise because being watched enables the possibility of communication (Hamilton & Lind, 2016), engages the sense of self (Conty et al., 2016) and motivates participants to manage their reputation (Tennie et al., 2010). All of these require mentalising processes, and this list of effects illustrates how changing a task from simple perception to a potential interaction with another person (even if the other is only a passive observer) can have a substantial impact on social cognition.

Differences in brain activity patterns are also seen between when participants are no longer alone in the MRI scanner. Direct gaze from another person (as opposed to a photo of eyes) engages medial prefrontal cortex (Cavallo et al., 2015), while the belief that someone is watching you can increase arousal (Myllyneva & Hietanen, 2015) and also engage mPFC (Somerville et al., 2013). An innovative series of studies created an eye-tracking task whereby participants could experience joint attention with a virtual human in fMRI, that is, the participant could look towards an object and the virtual human would look with them (or not) in a gaze-contingent fashion, giving a subjective experience of shared attention toward the gaze target. Trials where the participant engages in joint attention led to activation in the mentalizing network including mPFC (Schilbach et al., 2010). Thus, when participants experience more interactive social contexts in MRI, more engagement of mentalizing networks of the brain is seen.



These kind of results have motivated the move into hyperscanning (King-Casas et al., 2005) where neuroimaging data is captured from two or more participants simultaneously. While this can be implemented in fMRI (Koike et al., 2019), the options for natural social behaviour in the scanner are very limited. EEG and fNIRS (functional near-infrared spectroscopy) allow for a much wider range of natural social interaction behaviours. For example, EEG signals are coherence between infants and adults engaged in interactions (Leong et al., 2017). Using fNIRS, studies have found that two people engaged in a task together show coherent activity between their brains (Cui et al., 2012; Fishburn et al., 2018), with signals most commonly recorded from prefrontal cortex. Mutual eye contact between people (Hirsch et al., 2017) and conversation together (Jiang et al., 2015) as well as cooperation in multi-person economic games (Yang et al., 2020) can all lead to interbrain coherence.

However, it is still not straightforward to understand the mechanism of these effects, and to distinguish genuine interactions from common responses to the shared environment (Burgess, 2013). Progress can be seen in a study of interbrain coherence in interacting mice (Kingsbury et al., 2019) which identified neurons in the prefrontal cortex of mice which predict the individuals own behaviour and others which predict the behaviour of the partner mouse. Summing activation patterns across these neurons reveals a strong coherence across the two mouse brains. Thus, if both mice in a pair are engaged in mutually predicting their partner's actions, this individual mechanism can give rise to cross-brain coherence at a global level (Kingsbury et al., 2019). The same is likely to apply in humans (Hamilton, 2021), and gaining a greater understanding of how mutual prediction works and how we can integrate brain and behavioural data in the study of social interaction is likely to advance this area.

In the study of human interaction, it is worth noting that the vast majority of neuroimaging studies explore social perception or social interactions with strangers who typically provide a 'neutral' and easy-to-control stimulus. However, real world social relationships develop over years with known people and much deeper emotional connections. A small number of studies have examined the interaction of parent and child (Feldman, 2016) or romantic partners (Pan et al., 2017). Others have examined general groups of people, for examine those who are socially stigmatized (Krendl et al., 2006) or who are outgroup members (Harris & Fiske, 2006). Further work on meaningful social relationships could reveal a more complex picture of neural mechanisms that our current studies of strangers.

## Section 7: Summary

This chapter has reviewed four major brain networks that have a core role in human social interaction, for social perception, mentalising, action and emotion. While these networks can be

segregated in specific cognitive tasks, there is also evidence that these work together in interactive contexts. Rapid advances in real-world neuroscience have great promise for understanding interactive social behaviour, and also for applying our knowledge of social cognition to the wide range of neurodevelopmental disorders and mental health conditions which impact on social functioning. Future work examining the dynamics of brain mechanisms for social interaction and the role in more complex relationships between people is likely to be important in the future.

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